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Temporal and spatial overlap in the mate-locating behavior of two species of *Junonia* (Nymphalidae)

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Abstract. In northeastern Australia, males of two species of *Junonia*, *J. villida* and *J. orithya*, use a sit-and-wait tactic to detect females at encounter sites. In a brief study of the behavior of both species, I documented considerable overlap in the locations of the encounter sites used by males and in the time of day at which males were at encounter sites. Because of this overlap interspecific interactions are frequent, but males of *J. villida* at least respond much more strongly to conspecific males than to males of *J. orithya*. The discussion focuses on the lack of divergence in the mating behavior of these sympatric species.

Introduction

Males of many insects use landmarks such as hilltops or open areas along paths as places to encounter receptive females (Thornhill and Alcock, 1983). These landmarks typically do not contain any resources of material benefit to females but are instead places where receptive females appear primarily to mate. Some landmarks are used at the same time by a variety of species many of which are highly territorial. For example, Alcock (1987) found convergence in the spatial and temporal structure of male mate-locating tactics of a diverse set of hilltopping insects including a pompilid wasp, a bot fly, and representative of all families of butterflies (Alcock 1984, 1987; Alcock and O'Neill, 1987). However, there have been few studies that deal with the issue of what happens when closely related species, similar in overall morphology and behavior, share encounter site preferences. The general expectation is that selection will favor male behavior patterns that reduce the costs in terms of energy and distraction arising from interactions with other species. Brown and Alcock (1990), Hafernik (1982), Turner (1990), and Pinheiro (1990) all reported spatial segregation of butterfly species that concurrently utilize similar encounter sites. Moreover, Callaghan (1982) indicates that hilltopping Neotropical butterflies in 10 riodinid genera are temporally as well as spatially segregated.

In the Indo-Australian region, two species of *Junonia* Hubner, *J. villida* Godart and *J. orithya* Butler, have similar distributions and habitat preferences (Common and Waterhouse, 1982). Moreover, published reports (Heinrich 1972) and my preliminary observations indicated that males of these species utilize mate-locating tactics similar to those seen in *J. coenia* Hubner in North America (Hafernick 1982, Scott 1975b). Males perch in open areas of bare ground and fly up at passing conspecifics and heterospecifics. This brief study was designed to determine if the males of these two sympatric species are spatially and

temporally separated and if males respond more vigorously to conspecifics than they do to heterospecifics. A stronger response to conspecifics is expected for two potential reasons. First, males might be expected to make an effort to remove potential competitors from their perching locations. Heterospecifics are not mating competitors, so a stronger response should be directed at conspecifics (Brown and Alcock, 1990). Second, conspecific males may be more likely than heterospecific males to be misidentified as females when approached (Scott, 1975a) and then be chased and courted in error, especially given the low level of sexual dimorphism in these species (Common and Waterhouse, 1982).

Methods

The data were collected between 14 June and 6 July 1989 in an open eucalypt woodland on the campus of James Cook University of North Queensland, Townsville, Queensland, Australia. A census route, that was 600 m in length and followed a dirt road through the bush, was walked hourly to establish the distribution of perched males along the road and the daily timing of male activity.

In addition, observations were made on interactions between perched *J. villida* males and butterflies flying by their perch. The durations of these interactions were measured with a handheld stopwatch from when the males came within 2-3cm of one another until they separated. The form and outcome of the interactions was recorded immediately following the observation.

The census route sloped very gently uphill to the north except for a dip near the middle of the route where a small stream crossed the road. The only other major features were a small road that branched off to the west from the census route at about 200 m from the north end and a few large trees overhanging trees at 60, 240, and 330 m from the north end. The overhanging vegetation cast partial shade and was at least 15 m above the surface of the road.

All parametric summary statistics are given as the mean ± one standard error of the mean (SEM). Statistical comparisons were evaluated at the 0.05 level of significance.

Results

Males of the two species overlapped both in terms of the timing of their perching activity and the spatial distribution of preferred perch sites. In both species males were found perched on the road between 10:00 AM and 15:00 PM and the largest number of males of both species was found on the road between noon and 15:00 PM (Fig. 1).

Neither species was uniformly distributed along the census route (Fig. 2). Males of *J. villida* were seen perched in only 25% of the 30m segments along the census route. Similarly, *J. orithya* males were seen in only 40% of the 20 segments. Also, males were not uniformly distributed among those segments in which they were seen perched (*J. villida*: $\chi^2 = 13.6$, 4 df, $p = 0.009$; *J. orithya*: $\chi^2 = 21$, 7 df, $p = 0.004$). Males of the two species were distributed differently among those segments where at least one species was observed ($\chi^2 = 26$, 9 df, $p = 0.002$). Only one of the species was seen in those segments where less than 2 males were seen during the 19 censuses. Nonetheless, there was a great deal of overlap in their distri-

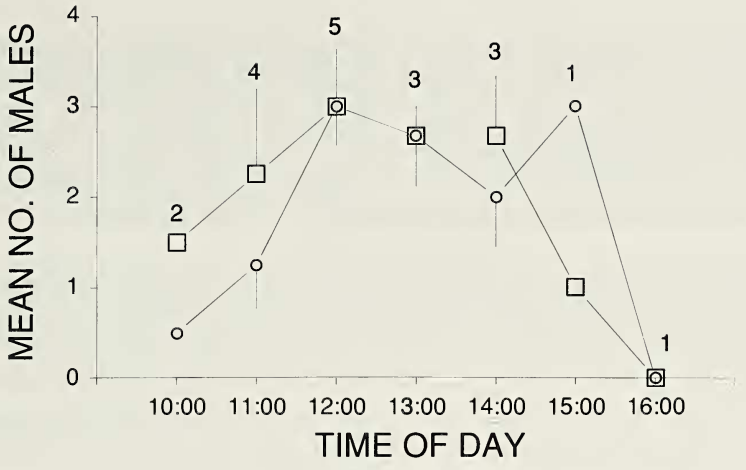

Fig. 1. The relationship between the mean number of males seen perched along the census route and time of day (*J. villida*, squares and positive error bars (1 SEM); *J. orithya*, circles and negative error bars (1 SEM)). The number of censuses from which the means and SEMs are calculated is shown above each time period.

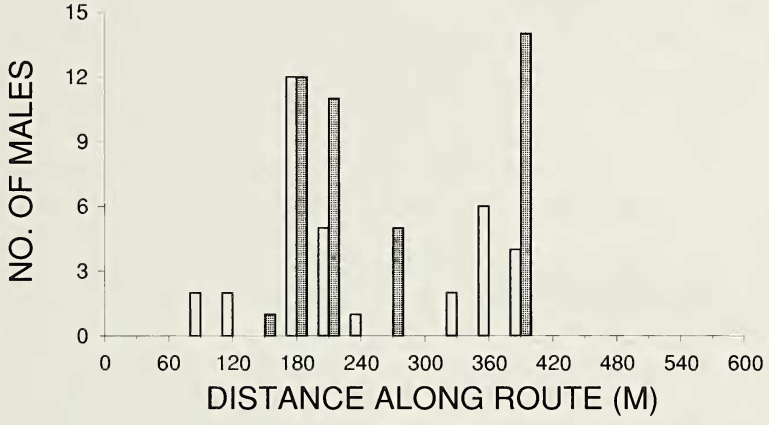

Fig. 2. The relationship between the total number of males seen perched in a 30 m stretch of the census route in 19 censuses and the distance along the census route (open bars, *J. orithya*, filled bars, *J. villida*). The bars for each 30 m segment are above the distance at the end of the segment away from the northern end of the route.

butions; for example, that part of the route at 150-210 m was popular with both species and in this and other overlap areas there was no evidence of spatial segregation with 30m segments. Males of both species were often seen perched within a meter of one another.

Males of both species flew up from their perches and approached both conspecifics and heterospecifics. Detailed observations were made on the form and duration of interactions between perched *J. villida* males and

congeners. An interaction with a conspecific typically began when a perched male flew up and chased a conspecific flying overhead. The two males then began flying rapidly around one another while gaining altitude. At a height of 3 m or so the two males quickly separated and one flew off while the other returned to the area and perched. Ten interactions of this sort that were timed lasted 3.99 + 0.398 sec (range = 2.1 - 6.4 sec).

Interactions between perched *J. villida* and *J. orithya* males flying overhead always ended very soon (1.55 + 0.184 sec, range = 1.2 - 2.6 sec, n = 8) after the two came into close contact. These interactions were significantly briefer than those between *J. villida* males (Student's t = 5.11, 16 df, p = 0.0001) and never led to an ascending flight. If both males had perches nearby, both usually returned to these sites after the interaction.

Discussion

The data suggest substantial overlap in when and where males of these two species sit-and-wait in their efforts to locate females, at least during the late autumn and early winter. This is in contrast to studies which have found clear divergence in the mate-locating tactics of males in a variety of sympatric butterfly species (Brown and Alcock, 1990; Callaghan, 1982; Pinheiro, 1990; Turner, 1990), including two New World species of *Junonia* (Hafernik 1982). This lack of divergence in the behavior of the closely related sympatric species suggests that (1) spatial and temporal distributions of receptive females in the two species are similar and (2) the potential costs of interspecific interference are relatively low (Rutowski (1991)).

At this point little is known about the behavior and ecology of receptive females in these species and the factors that might affect their distribution. In both species the larvae are polyphagus and feed on a wide range of similar foodplants (Common and Waterhouse, 1982) which might produce similar spatial patterns of emergence in these species. Also, females may mate more than once in *J. villida* and other members of the genus (Ehrlich and Ehrlich, 1978; Scott, 1975a). Similarities in patterns of female receptivity may also contribute to interspecific similarities in the distribution and abundance of receptive females.

Males may gain little by adopting distinct perch sites because the costs of interspecific interactions appear to be small, at least under the conditions that applied during this study. These costs would be determined by the frequency of interactions with heterospecifics as well as the form that such interactions take. Although no measures were made of interaction rates in this study; interspecific interactions were frequently observed. Indeed, males indiscriminately approach just about anything passing nearby, including birds, other insects, and thrown rocks. However, after the initial approach males of at least *J. villida* males respond to males of *J. orithya* less intensely that they do to conspecifics. In this

way, males apparently minimize the time spent interacting with heterospecific males and there is then no strong selection that favors the differential utilization of encounter sites by these species. It would be of interest to see if male behavior diverges when conditions such as higher population densities of both species produce conditions that increase the costs of interspecific interactions.

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